

The University of Chicago

THE RELATION BETWEEN FREQUENCY
INDEX AND ABUNDANCE AS APPLIED
TO PLANT POPULATIONS IN A
SEMIARID REGION

A PART OF A DISSERTATION SUBMITTED
TO THE FACULTY OF THE DIVISION OF
THE BIOLOGICAL SCIENCES FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1932

By
WILLIAM GROVENOR MCGINNIES

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THE RELATION BETWEEN FREQUENCY INDEX AND ABUNDANCE AS APPLIED TO PLANT POPULATIONS IN A SEMIARID REGION

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The problem of determining the relative or absolute abundance of the component plants of both small and large communities is of great importance for adequate analysis of ecological relationships. Chart and list quadrats of various sizes, transects, and other means of sampling have provided considerable information for small areas, but do not entirely serve the needs where the stand or community under study has a wider range. As it is obviously impracticable to count the number of individuals of each species within a large community, many workers have turned their attention to some rapid method of sampling. Probably the most common system used is the "frequency index"¹ method of Raunkiaer ('09, '18). This investigator marked off a number of plots (usually 25) one-tenth of a square meter in area. The species present on each area were noted but the individuals were not counted. The percentage of plots on which a species occurred was designated as its frequency per cent.

Since this pioneer work by Raunkiaer, many investigators have tested the method under a wide range of vegetative conditions throughout the world. The methods used and the results obtained by Raunkiaer were made more available to English-speaking workers through translations by Smith ('13) and by Fuller and Bakke ('18). The investigators who have used and discussed this method include: Arrhenius ('21, '22, and '23), Gleason ('18, '20, '22, '25, and '29), Kenoyer ('27), Hanson and Ball ('28), Hanson and Love ('30), and Romell ('30). The general consensus of opinion seems to be that it furnishes a good basis for the comparison of plant communities, although there has been some discussion as to its degree of accuracy and its possible variations.

The present study was undertaken with the purpose of testing the method under semi-arid conditions, and, if it proved basically sound, to use it for comparison of changes occurring within certain plant communities, and for a means of comparison between plant communities of different habitats. The present paper is devoted to a consideration of the literature and a presenta-

¹ "Frequency index" is used here as the equivalent of "frequency" and "frequency per cent" of some of the earlier papers dealing with this subject. The term "frequency index" is used, as the values obtained by this method are indices of frequency rather than exact frequency values.

tion of the experimental results pertaining to the relation of frequency index to abundance. The size and number of quadrats which would yield the most reliable information were given some consideration, but the principal aim has been to determine as nearly as possible the exact relationship between frequency index and abundance if any such definite relationship should exist.

NUMBER OF QUADRATS NECESSARY FOR SIGNIFICANT RESULTS

Within a given stand of vegetation of a normal degree of homogeneity, each additional quadrat should decrease the average deviation. Beyond a certain point, however, additional quadrats will not reduce the deviation sufficiently to justify the labor expended. The determination of this number depends in part on the heterogeneity of the stand of vegetation, and in part on the standards of accuracy set by the investigator.

Raunkiaer thought that 25 to 50 quadrats located in a straight line gave the optimum results when time and accuracy were both considered. Gleason ('20) recommends that the homogeneity of the community should be taken into consideration in making a decision as to the number of quadrats to be used. If possible, 100 should be tallied. The number would be dependent in part on the size of quadrat used. Large quadrats would include a greater number of species and hence fewer quadrats would be needed to furnish adequate frequency index figures for the less abundant species. Kenoyer ('27) concluded that 25 quadrats gave essentially the same results as a larger number. Hanson and Ball ('28) used 50 quadrats to represent each condition in their studies of the influence of grazing on the composition of vegetation. Later, the same investigators used 30 quadrats of various sizes in a similar study. In all the work cited above, the number of quadrats used was more or less arbitrarily chosen to fit the conditions under observation.

In the present study, the number of plots to be used was calculated on the basis of chance distribution. In the majority of cases the quadrats were evenly distributed over an area of 10,000 sq. m., so that the number of quadrats of various sizes to give the required accuracy could be computed. As a recorded frequency index cannot be less than 1, the lowest possible frequency index (expressed in per cent) for 25 quadrats would be 4, and for 50 quadrats would be 2. This tends to accentuate the deviations, but in addition to this, it was found that under the experimental conditions there was a decrease in the deviation between comparable frequency indices with an increase in the number of quadrats used.

In all determinations, at least 100 quadrats were recorded and in the majority of cases 200 quadrats in two series of 100 each were tallied. An increase in accuracy was obtained up to 200, but above 100, it is doubtful if the increase sufficiently compensated the time expended.

THE RELATION BETWEEN FREQUENCY INDEX AND ABUNDANCE
UNDER IDEAL CONDITIONS

There has been considerable discussion as to the relation of frequency index to abundance. Some have assumed that the frequency index is directly proportional to abundance, while others, notably Gleason ('20), Arrhenius ('21), and Romell ('30), believe that it is not. They indicate, however, that the relation between frequency index and abundance can be more or less accurately expressed by curves or equations.

In order to test the mathematical relations between frequency index and abundance and to determine the amount of variation under ideal conditions, a simple laboratory test was made. It was planned that the laboratory test should possess the same proportions as the work in the field, that is, a square centimeter would be equal to a square meter in the field. For these tests, a table was constructed with a cloth-covered square top one square meter in area, with a ridge or shoulder completely surrounding the top. Beads of different colors, each color representing a different abundance, were evenly sprinkled over the top to secure a reasonable random distribution of each color. A 10 sq. cm. square frame with a 1 sq. cm. compartment inserted in one corner was constructed. This double frame was used to mark off simultaneously areas of 10 and 1 sq. cm. for frequency index determinations. The table top was marked with easily visible guide dots in two series of 100 each. The *A* series was evenly spaced in 10 rows of 10 each and the *B* series located at equally distant points on the diagonals of the *A* series. After the beads had been distributed, the double frame was set down squarely with a dot in its center and each different colored bead present within each frame was checked on an appropriate form. The records for the 10 sq. cm. frame and the 1 sq. cm. frame were kept separately. No record was kept of the *number* of beads within the frames but merely whether or not one or more beads of given color were present. This was repeated successively for each guide dot in the *A* series, then in the *B* series. The beads were then collected and redistributed and the sampling repeated. The purpose of running two sample series each time the beads were distributed was to check the regularity of distribution. As the records for each quadrat were kept separately, irregularities could be checked. The calculations used here were based on 10 repetitions each of the *A* and *B* sample series. The results obtained are shown in table I.

Table I shows that there is a distinct difference between the total number of beads which might be expected to lie within the areas represented by a sample series and the corresponding frequency index. For example, the area of the table top is 10,000 sq. cm. and the total area represented in a series of 100 10 sq. cm. samples is 1000 sq. cm. With perfect random distribution, there should be 1000 brown, 500 orange, 250 lavender, 120 black, 100 red, 80 gold, 50 yellow, 30 green, 20 pink, and 10 blue beads within this area. On this basis the brown, orange, lavender, black, and red might be expected to

TABLE I. *Frequency index for a given number of beads distributed at random, on an area of 10,000 sq. cm.*

Color of beads	Number of beads	Mean frequency index	Mean frequency index
		for 10 sq. cm. quadrats	for 1 sq. cm. quadrats
Brown	10,000	100 $\pm$ 0.024	64 $\pm$ 0.401
Orange	5,000	99 $\pm$ 0.083	42 $\pm$ 0.443
Lavender	2,500	90 $\pm$ 0.401	22 $\pm$ 0.388
Black	1,200	69 $\pm$ 0.521	12 $\pm$ 0.302
Red	1,000	62 $\pm$ 0.362	10 $\pm$ 0.350
Gold	800	55 $\pm$ 0.531	8 $\pm$ 0.252
Yellow	500	40 $\pm$ 0.432	5 $\pm$ 0.229
Green	300	26 $\pm$ 0.350	4 $\pm$ 0.202
Pink	200	17 $\pm$ 0.262	2 $\pm$ 0.147
Blue	100	10 $\pm$ 0.271	1 $\pm$ 0.092

give a frequency index of 100, but the experimental results show a frequency index approaching 100 only for the brown and orange beads. The frequency index decreases successively to 62 for the red which represents a very significant difference from 100.

The explanation of this difference may be found in the sampling method. If the average number of beads on the entire area is 1 on every 10 sq. cm. it would not mean that every area selected of 10 sq. cm. would have a bead on it. Even if the beads were perfectly spaced at 10 cm. intervals, it would be possible to turn a 10 sq. cm. frame so that it would not have any beads within it. If the total number of beads were counted on 100 quadrats, it would be found that some of the individual quadrats would show 2 or more beads while others would not have any. The total would closely approach 100. However, the frequency index method only measures the "hits" and "misses," and under the conditions outlined above there will be many "misses."

At the lower end of the scale there seems to be a closer correspondence between the total number of beads in 1000 sq. cm. and the frequency index. Random distribution would allow 10 blue, 20 pink, 30 green, 50 yellow, and 80 gold beads for the combined area of a sample series. The difference between these numbers and the mean frequency index varies from 0 for the blue to 25 for the gold beads in regularly increasing magnitude. The explanation for the closer approach of frequency index to the average abundance in lower frequency ranges is, that as the total number of individuals becomes less the average distance between beads is greater and hence the likelihood of more than 1 bead occurring on any given 10 sq. cm. area decreases. Thus the frequency index tends to give the same results as counting where the individuals are widely spaced.

The frequency indices for the 1 sq. cm. sample series show substantially the same thing in a smaller magnitude. The total number of beads on the 100 1 sq. cm. samples would approximate 100 brown, 50 orange, 25 lavender, 12 black, 10 red, 8 gold, 5 yellow, 3 green, 2 pink, and 1 blue. The frequency index is identical with the abundance (with one exception) up to an abundance of 12, beyond that, there is an increasing divergence between abundance and frequency index.

To determine the relation of frequency index (FI) to abundance, curves were plotted with abundance on the x -axis and the frequency index on the y -axis. It was found that the curves thus secured approximated the curve derived from the equation $FI = 1 - (1 - 1/q)^n$ suggested by Gleason ('20). This equation according to Gleason was used to determine the FI for n plants on q quadrats. Applying this to the bead data, the equation may be expressed as $FI = 1 - (1 - 1/100)^n$ or $FI = 1 - 0.99^{n/2}$ where $n = \text{Total beads}/10,000$ multiplied by the area represented in a sample series of 100 quadrats. Thus for computing FI for the lavender beads, n would equal $(2500/10,000) \cdot 1000 = 250$ for the 10 sq. cm. sample series and $(2500/10,000) \cdot 100 = 25$ for the 1 sq. cm. series. The essential difference in the equation as compared to its use by Gleason is in the calculation of n . Gleason counted the number of plants on 100 quadrats, while in the above case it is calculated on the average number per square centimeter. The relation of frequency index to total abundance as expressed by the equation is identical for both frames. The resulting curve is shown in figure 1. Total

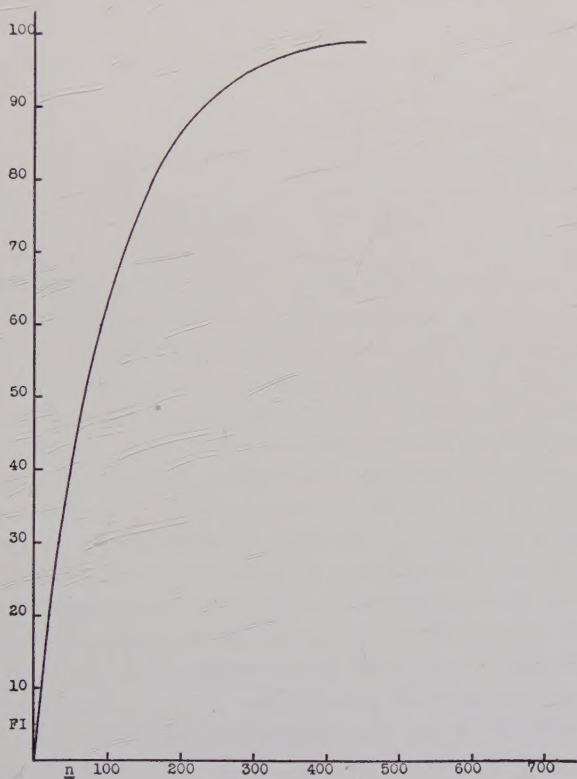


FIG. 1. Relation of frequency index to abundance. For total abundance, multiply by 10 for the 10 sq. cm. quadrats and by 100 for the 1 sq. cm. quadrats.

² The resulting quantities are usually expressed as whole numbers.

abundance for the entire area can be determined for the two sample series from the experimental frequency indices by multiplying the corresponding n by 10 for the 10 sq. cm. series and by 100 for the 1 sq. cm. series. The degree of fit to the calculated curve was determined by computation of the residuals, standard error, alienation and correlation indices, as suggested by Bruce and Reineke ('31). The essential data for these calculations are given in table II.

TABLE II. *Comparison of experimental frequency index for beads with values obtained from curve*

10 sq. cm. quadrats					1 sq. cm. quadrats				
n	Exp. FI	Curve FI	Diff.	Diff. sq'd	n	Exp. FI	Curve FI	Diff.	Diff. sq'd
10	10	10	0	0	1	1	1	0	0
20	17	18	-1	1	2	2	2	0	0
30	26	26	0	0	3	4	3	+1	1
50	40	40	0	0	5	5	5	0	0
80	55	55	0	0	8	8	8	0	0
100	62	63	-1	1	10	10	10	0	0
120	69	70	-1	1	12	12	11	+1	1
250	90	92	-2	4	25	22	22	0	0
500	99	99	0	0	50	42	40	+2	4
1000	100	100	0	0	100	64	64	0	0
Total	568	573	-5	7		170	166	+4	6
Avg.	56.8	57.3	-0.5	0.7		17.0	16.6	+0.4	0.6
Standard error				0.84	Standard error				0.77
Alienation index				0.027	Alienation index				0.039
Correlation index				0.99	Correlation index				0.99

The figures in the columns marked "difference" represent the departure of the experimental frequency indices from those calculated from the curve. The average difference in both quadrat series is less than 1 bead, minus in the 10 sq. cm. quadrat series and plus in the 1 sq. cm. quadrat series. Although the sum of the differences should be zero with a perfectly fitted curve, the deviations are well within the possibilities of experimental error, so that the equational curve was adopted as the standard.

Having thus established the relation between frequency index and abundance under conditions of rather ideal random distribution, and having determined that the equation suggested by Gleason was fundamentally sound, experiments were then conducted in the field to determine whether or not these basic relationships existed under the average distribution of species and individuals in the various plant communities.

In preliminary field tests, quadrats with areas of 0.1, 0.25, 0.5, 1, 2, and 10 sq. m. were tried in numbers ranging from 25 to 200. The large quadrats, however, did not give an adequate range in frequency indices for the determination of the relative abundance of the more common species. It was found that the 1 and 2 sq. m. quadrats gave the best range of frequency

indices for the greatest number of species, but that the species with the greatest abundance were differentiated much better, as to relative abundance, by the smaller quadrats. On the basis of these results, it was decided to use quadrats of 1 sq. m. and 0.1 sq. m. for the field determinations of the relation between frequency and abundance. A suitable square meter frame was constructed of $\frac{1}{2}$ in. pipe with a 0.1 sq. m. frame set in one corner, so that the 1 sq. m. quadrats included the 0.1 sq. m. quadrats. Each series of 100 quadrats was laid out at regular intervals within a square area 100 m. on a side. The 1 sq. m. quadrat series would then represent a 1 per cent sample and the 0.1 sq. m. series would represent a 0.1 per cent sample. On the basis of the bead results, 100 1 sq. m. quadrats, evenly distributed over an area of 10,000 sq. m., should include all species with an abundance of 100 or more, and to furnish more or less significant frequency indices for species with an abundance up to 50,000; and 100 0.1 sq. m. quadrats should give significant frequency indices for species ranging in abundance from 1,000 to 500,000. The entire range of frequency indices would thus include all plants with an average abundance of 1 plant on 100 sq. m. to 50 plants on 1 sq. m.

The field method was based on that used with the bead tests, that is, square plots 100 m. on a side were laid off, then starting 5 m. south and 5 m. east of the northwest corner, 100 quadrats were located in 10 north and south rows of 10 each. This was designated as sample series *A* and, in most cases, a sample series *B* was run east and west, starting from 10 m. north and 10 m. east of the southwest corner. In this way the two sample series were entirely independent, but so arranged that they should be strictly comparable. The usual method was to locate each line of quadrats by means of stakes or flags and to locate the quadrats by pacing. Each time that a quadrat was located, the frame was set squarely in front of the operator, just touching his toes and with the 0.1 sq. m. inset frame always on the right hand corner nearest the operator. Records were kept on a special form on which a block of 100 numbered squares was used for each species, and if the species were present on a given quadrat, an x was placed in the square on the form corresponding to the number of the quadrat. By this means, irregularity in the distribution of any species could be checked. Plants rooted within the area marked off by the frames were marked with an x on the form, and overhanging plants were designated with a small circle. Only the x 's are used in the basic calculations. Frequency index data were collected on 41 different plots located in various parts of Arizona. On 27 plots, both sample series *A* and *B* were run; on the other 14 plots, only one sample series was run. Frequency index determinations were repeated twice for 6 series and three times for 12 series, in different years, making a total of 98 determinations of 100 for both the 1 sq. m. and 0.1 sq. m. quadrats. On some of the sample plots, counts were made of the number of individual plants of some of the representative species. In each case, all the individuals of a given species were counted on both the 1 sq. m. and 0.1 sq. m. quadrats for the entire series of 100 quadrats. Alto-

gether, 298 plants on the 1 sq. m. and 277 on the 0.1 sq. m. were counted. The species to be counted were selected on the basis of ease of counting and representation of the entire range of frequencies. Not more than 10 species were selected on any one plot.

The vegetation in which the plots were located varied from desert grassland to yellow pine forest and might be divided into three general zones: Desert Grassland, Intermediate, and Yellow Pine Forest.

The Desert Grassland in Arizona lies mostly between elevations of 2000 to 4000 ft., with a rainfall of 12 to 18 in. Characteristic plants include: *Rothrox grama*, *Bouteloua rothrockii*, black grama, *B. eriopoda*, mesquite, *Prosopis velutina*, and several species of *Aristida*.

The Intermediate zone includes short grassland, chaparral, sagebrush, and pinon-juniper woodland, lying between elevations of 4000 to 6800 ft., with annual precipitation of 15 to 22 in. The short grassland is characterized by blue grama, *Bouteloua gracilis*; the chaparral by oaks, *Quercus turbinella*, and others, and mountain mahogany, *Cercocarpus* spp.; the sagebrush communities by the mountain sagebrush, *Artemisia tridentata*; and the pinon-juniper woodland by pinon pine, *Pinus edulis*, and junipers, *Juniperus utahensis* and *J. monosperma*.

The Yellow Pine Forest, characterized by western yellow pine, *Pinus ponderosa*, lies between elevations of 6800 to 8000 ft., with an annual precipitation above 25 in. Among the important herbaceous species in this zone are several grasses, such as Arizona bunch grass, *Festuca arizonica*, mountain bunch grass, *Muhlenbergia gracilis*, and a wide variety of herbaceous dicotyledons.

For more complete descriptions of these plant communities, reference may be made to Shantz and Zon ('24), and Hanson ('24).

In general, areas with dense shrubby growth were avoided. Except for this, plots were chosen to be as nearly representative of the major plant communities as possible. In all three zones, it was also possible to select more or less natural areas and some that had been more or less changed by grazing, lumbering, or fire. In nearly every case, the density of vegetation was rather low and in only one or two cases did it approach a sod, or similar complete ground cover. The density of herbaceous vegetation was lowest in the desert grassland and highest in meadow-like communities of the yellow pine zone.

The number of the sample series located in each of these zones was: Desert Grassland, 65; Intermediate, 9; Yellow Pine Forest, 24. The 98 sample series yielded a total of 3396 frequencies for the 1 sq. m. quadrats and 2420 for the 0.1 sq. m. quadrats. On the basis of the 1 sq. m. series, there was an average of 35 species for each plot. The average number for the 0.1 sq. m. series was 25. These species showed a wide range in frequency index as indicated in table III.

Of the total number of species found on the 1 sq. m. series, 28.7 per cent were not represented in the corresponding 0.1 sq. m. series, otherwise, the

TABLE III. *Distribution of frequency indices by classes*

Frequency index	Per cent of total	
	1 sq. m. series	0.1 sq. m. series
0	0.0	28.7
1- 5	39.9	29.2
6- 10	11.9	16.5
11- 15	7.3	6.1
16- 20	5.2	4.2
21- 25	4.4	2.9
26- 30	3.5	2.4
31- 35	2.9	1.8
36- 40	2.1	1.1
41- 45	2.2	1.5
46- 50	1.8	0.8
51- 55	1.8	0.8
56- 60	2.3	0.7
61- 65	2.0	0.6
66- 70	2.4	0.6
71- 75	2.0	0.7
76- 80	1.6	0.5
81- 85	1.6	0.2
86- 90	1.8	0.2
91- 95	1.9	0.2
96-100	1.3	0.2

proportional distribution is very similar. If the 0.1 sq. m. series includes only 71.3 per cent of the species in the 1 sq. m. series, the question may be raised as to whether or not the frequency index figures represent the total population for the 10,000 sq. m. plot. They do not include the entire population, but they do include the major portion. Check observations in each case showed that the majority of species were included and that only the rarer species were missed.

There has been considerable discussion as to the relative abundance of the individuals of various species in any given plant community as indicated by frequency index studies. Raunkiaer ('18) found that if the various species present be grouped into frequency classes of 20 each, designated as A, B, C, D, and E, representing frequency indices of 1-20, 21-40, 41-60, 61-80, and 81-100, the per cent of the total species falling in each class may be expressed as $A > B > C \cong D < E$. Thus, 8078 frequency indices gave the ratio 53, 14, 9, 8, 16. Kenoyer obtained similar results on the basis of 1425 frequency indices from the region around Lake Michigan. He notes a tendency for Class A to be larger and Class E smaller than in Raunkiaer's study. He attributes this to the less stabilized condition of the communities studied. Kenoyer also notes that where the number of species is small, they tend to be confined to Classes A and E.

Hanson and Ball ('28) found that under deferred grazing the frequency index ratio of 62, 14, 7, 7, 10 approached those of Raunkiaer and Kenoyer, but that under continuous grazing there was an increase in Classes C and D, largely at the expense of Class E. Hanson and Love ('30), using quadrats of

different sizes, found that the percentage of species in Class A was always greatest but that the percentage in this class decreased with an increase in the size of the quadrat. An increase in the number of species falling in Class E, as compared to Class D, was shown for the 0.25, 2, and 3 sq. m. quadrats in a continuously grazed pasture and the 4 sq. m. quadrats in the pasture under deferred grazing.

In table IV, the distribution of the various species by frequency classes in the present study is compared to those obtained by Raunkiaer, Kenoyer, and Hanson and Ball.

TABLE IV. *Comparison of frequency indices by classes*

	Total number of frequency indices	Class percentages				
		A	B	C	D	E
Raunkiaer	8078	53	14	9	8	16
Kenoyer	1425	70	12	6	4	7
Hanson and Ball						
Deferred pasture	42	62	14	7	7	10
Continuously grazed pasture	47	59	13	13	11	4
Arizona, meter	3396	64	13	8	8	7
0.1 meter ³	2420	79	12	5	3	1
0.1 meter ⁴	3396	85	8	4	2	1

³ Based on the frequency indices recorded for 0.1 sq. m. quadrats.

⁴ Based on all frequency indices. Class A would include all frequency indices from 0-20.

The frequency indices included in the Arizona studies represent several conditions of grazing and protection from grazing, and variations in ecological conditions such as desert, grassland, and coniferous forest, but in all cases the density of vegetation is relatively low.

It would appear from these data that the ratio of frequency classes is not a constant for all conditions and all methods of obtaining frequency indices. The ratio is more of an expression of the relation between dispersal of individual plants and the size of quadrat used. Raunkiaer, working in a rather dense stabilized vegetation, obtained a certain ratio with 0.1 sq. m. quadrats. Kenoyer ('27, p. 344) found it necessary to increase the size of his quadrats to obtain the same ratio in certain communities. Hanson and Ball obtained the same ratio with 2 sq. m. quadrats in the less dense vegetation of Colorado. The ratios for the 1 sq. m. quadrats in the relatively sparse plant populations of Arizona approach the Raunkiaer ratio, but the 0.1 sq. m. quadrats show a steady decline in percentage, from an extremely large group in Class A, to 1 per cent in Class E. It is perfectly conceivable that the area of the quadrats could be altered so as to either reduce the percentage of species in Class E to zero, or, on the other hand, to throw all or almost all into Class A. Reducing the size of the quadrats will bring about an increase in the classes of lower frequencies and increasing the size of quadrats will increase the percentage

of species falling in the higher frequency classes. Gleason ('20) recognized this and suggested a formula for determining the size of quadrat which would include all species of a given abundance. Gleason ('29) showed further that these classes do not represent equivalent groups on the basis of abundance. This relationship is indicated in figure 1, which shows that the higher frequency index classes include a much greater range in abundance than do the lower. Gleason ('29) also pointed out that the ratio as expressed above will obtain only when quadrats are of such size as to include all species present in the five groups, and that "Raunkiaer's law is merely an expression of the fact that in any association there are more species with few individuals than with many. . . ."

THE RELATION BETWEEN FREQUENCY INDEX AND ABUNDANCE UNDER AVERAGE FIELD CONDITIONS

It has been shown that with good random distribution, the frequency index offers a good measure of abundance. Mathematically, the method is sound, provided that the population examined is one in which the individuals are independently distributed at random in accordance with the law of chance. If

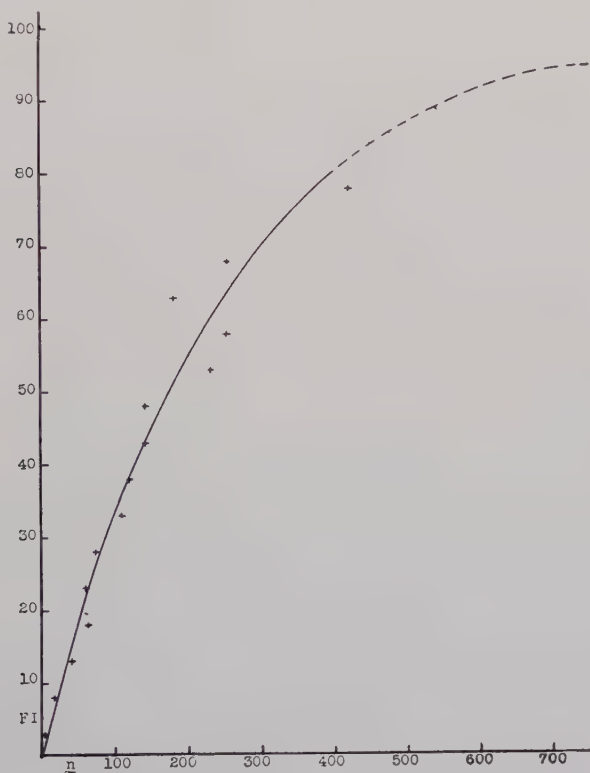


FIG. 2. Relation of frequency index to abundance for the 1 sq. m. quadrats.

the individuals of the various species are independently distributed at random, the relationships determined in the laboratory should hold in the field; if they are not distributed at random, the general principle might still hold within reasonable limits, provided that the irregularities are of such a nature as to be subject to mathematical treatment.

Many investigators, including Gleason ('20) and Arrhenius ('21), believe that in general the individuals of a given species represent a random distribution, while others, notably, Romell ('30), believe there is a tendency for over and under dispersal. Gleason ('20), while believing in random distribution,

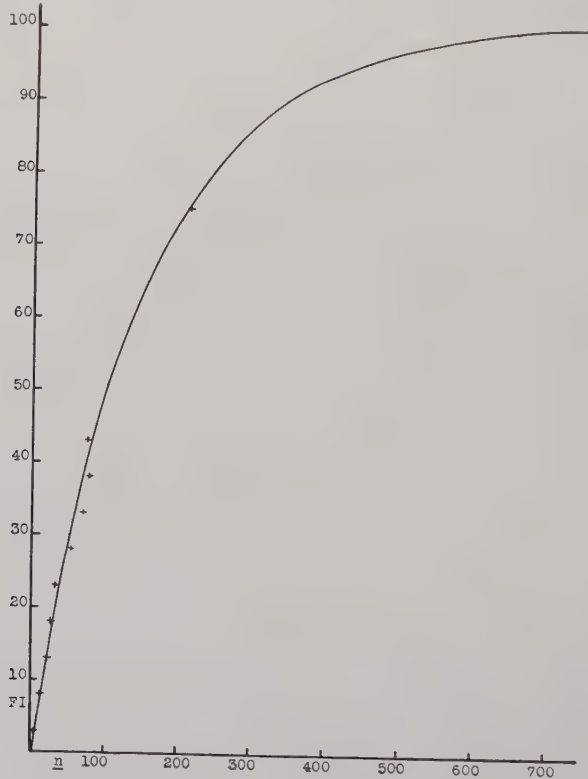


FIG. 3. Relation of frequency index to abundance for the 0.1 sq. m. quadrats.

does recognize irregular distribution in unstabilized communities and ('29) for plants propagated vegetatively. He ('20) also states that "It is not possible to draw any accurate conclusions as to the relation between theoretical and actual number of individuals, but in general, the theoretical number is one-fifth to two-thirds as large as the actual. . . ."

One of the objects of the present study was to determine if actual abundance could be calculated from frequency indices. The first step was to determine the degree of correlation between frequency indices and actual abun-

dance. On the basis of 298 counts, each representing the total abundance of a given species on 100 quadrats from representative plots, correlation ratios for the 1 sq. m. quadrats were found to be $\eta_{xy} = 0.8553 \pm 0.0105$ and $\eta_{yx} = 0.8302 \pm 0.0121$. The corresponding correlation ratios of the 0.1 sq. m. quadrats were $\eta_{xy} = 0.8357 \pm 0.0122$ and $\eta_{yx} = 0.8753 \pm 0.0095$. With such a high degree of correlation, it would appear that the relation between frequency index and abundance might be subject to mathematical treatment. When the curves for these relationships are plotted (figs. 2 and 3), it is seen that they have the same general form as that shown in figure 1, but that the slopes of the curves are not the same. However, in each case the experimental curve very closely approximates an equational curve such as that suggested by Gleason. In the case of the curve for the 1 sq. m. quadrats, there is a marked tendency for the frequency index values for any given abundance to fall below the equational curve for frequency indices between 70 and 100. There are not enough data available at the present time to determine whether this is due to some distributional factor or to errors in counting. For this reason, the upper portion of the curve is shown by a broken line.

The general trend of the curves representing the field data is toward a greater abundance of individuals for a given frequency index. In fact, for the 1 sq. m. series, the abundance indicated is 2.5 times as great for a given frequency index as that for a corresponding frequency index in the bead study, and the abundance for the 0.1 sq. m. series is 1.5 times that of the theoretical curve based on ideal random distribution. The curve equation in these cases becomes:

$$FI = 1 - (0.99)^{\frac{n}{2.5}} \text{ for the 1 sq. m. series, and}$$

$$FI = 1 - (0.99)^{\frac{n}{1.5}} \text{ for the 0.1 sq. m. series.}$$

Where n is the unknown, the equation becomes:

$$n = \frac{\text{Log } (1 - FI)}{\text{Log } 0.99} \text{ as applied to the bead results,}$$

$$n = 2.5 \frac{\text{Log } (1 - FI)}{\text{Log } 0.99} \text{ for the 1 sq. m. series, and,}$$

$$n = 1.5 \frac{\text{Log } (1 - FI)}{\text{Log } 0.99} \text{ for the 0.1 sq. m. series.}$$

The data obtained from the bead experiments representing random distribution indicate that the same basic equation could be used regardless of the size of the quadrat samples. They also indicate that the increase in abundance is proportional to the increase in area of the quadrat samples. In the results obtained from the field experiments, it is necessary to include a constant in the basic equation in order to construct suitable curves. This con-

stant is the same for all frequency index-abundance ratios as determined for a given quadrat size in a given type of vegetation, but is different for each different quadrat size and may vary with the type of vegetation under consideration. The above constants represent the average of 98 sample series located over a rather diverse vegetational range. All these plant communities have one thing in common, however, and that is that the vegetation is relatively sparse.

In order to determine the relation between abundance of the various species on the 1 sq. m. and 0.1 sq. m. quadrats, the correlation was determined, and the relation was found to be linear with a correlation coefficient $r = 0.8635 \pm 0.0103$, but instead of the ratio of abundance on the two areas being 1 to 10, it was approximately 1 to 7. It might be that this lowered ratio is due to deviations of insufficient number of samples and that the ratio should be 1 to 10. This does not seem to be probable, however. The deviations from the mean are large but not sufficiently large to account for such a difference. Furthermore, when abundance is predicted by frequency indices, using the equational curves, a close correspondence is found to this ratio; and when the ratio between the abundance on the 0.1 sq. m. series and the 1 sq. m. series is computed from these frequency indices, it is found to be 1 to 6.73. The explanation for a ratio of the number of individuals of approximately 1 to 7 on quadrats with a ratio of 1 to 10 in their respective areas is not readily apparent. With good random distribution in the bead experiments, the increase in number of individuals was directly proportional to the increase in area, but in the field the increase in the number of individuals is not directly proportional to an increase in area.

This difference might be due to over or under dispersal of individuals as pointed out by Romell ('30) provided that there was not a tendency for over dispersal and under dispersal to compensate when a large number of species are considered. Under the conditions of this experiment, irregular patches of bare ground were common, and it may be that the irregular distribution of the vegetation, alternating with these bare areas, would account for this lowered ratio. Further experiments are needed to furnish additional information before this problem can be definitely answered.

THE RELATION BETWEEN FREQUENCY INDICES OBTAINED FROM QUADRATS OF DIFFERENT SIZES

It has been pointed out previously in this paper that frequency indices vary in magnitude according to the size of quadrat used. Quadrats of different sizes will give entirely different ranges of frequency indices. The problem of the optimum size for quadrats has been considered by a number of investigators.

Raunkiaer ('09) tested quadrats ranging in size from 100 dm² to 1 dm² and decided that quadrats with an area of 0.1 sq. m. were most satisfactory.

Arrhenius determined by various calculations that the amount of deviation would be nearly inversely proportional to the area of the quadrat used, but that this larger deviation could be overcome by increasing the number of quadrats. He estimated that 200 tenth meter quadrats would give significant results. Gleason ('20) recognized the relation of size of quadrats to the frequency indices obtained, and gives formulae for calculating the size of quadrats necessary to obtain a quadrat which will include all the plants of a given frequency. He states that the optimum size is one in which there is a wide divergence of frequencies from 1 to 90 or even more. Kenoyer ('27) used quadrats varying in size from 0.1 sq. m. for dense herbaceous vegetation up to 100 sq. m. where only woody forms were considered. The size was adjusted so that a J-shaped curve was secured when the frequency indices were plotted according to the number falling in 5 classes (0-20, 21-40, 41-60, 61-80, 81-100).

Hanson and Love tested quadrats with areas of 0.25, 0.5, 1, 2, 3, and 4 sq. m. and decided that 1 sq. m. was the optimum size. They reached this decision largely because plotting the number of species against the size of the quadrat in square meters gave a curve with a tendency to flatten at 1 sq. m. This indicated that up to 1 sq. m. each addition in size of the quadrat would result in a considerable gain in the number of species included. The curve flattened out still more for 2 sq. m. but they concluded that when time was considered, the greatest efficiency would result from the use of 1 sq. m. quadrats.

Romell ('30) concluded that plants are not distributed at random and that very different results would be obtained by the use of quadrats of various sizes, and he recommended that 0.1 sq. m. be adopted as standard. On the other hand, Cain ('32) recommends that the size of the quadrat be adjusted to the purpose of the investigation and the character of the vegetation.

It follows, that if quadrats of different sizes are to be used by different investigators, the full value of such investigations will not be forthcoming unless there is some way of correlating the results obtained by the various investigators. It has already been shown that there is a high degree of correlation between the frequency indices obtained by quadrats of two different sizes under rather ideal conditions with beads. Under field conditions where there is a difference in the equation expressing the relation of frequency index for the 1 sq. m. and 0.1 sq. m. quadrats, the question might be raised as to whether or not a high degree of correlation existed. To determine this point, the correlation ratios were determined for 1511 paired frequencies ranging from 11 to 90 for the 1 sq. m. series and from 1 to 85 for the 0.1 sq. m. series. They were as follows: $\eta_{xy} = 0.8840 \pm 0.00379$ and $\eta_{yx} = 0.9092 \pm 0.00301$, indicating high positive correlation. Furthermore, when a curve is plotted to show the relation of the frequency indices of the 1 sq. m. quadrats to that of the 0.1 sq. m. quadrats (fig. 4), it is found that the curve is identical with that shown in figure 2 for predicting abundance from frequency index for the

1 sq. m. quadrats. That is, the relation between frequency indices for these two quadrat sizes is the same as the relation of the frequency index of the larger to its abundance divided by 10. This relationship was tested with the bead data and for a limited number of 0.1 sq. m. and 0.01 sq. m. quadrats, and for 10 sq. m. and 1 sq. m. quadrats, and was found to hold true in every case. It seems probable, therefore, that the relationship between frequency indices for quadrats is definite and subject to mathematical treatment. The relation

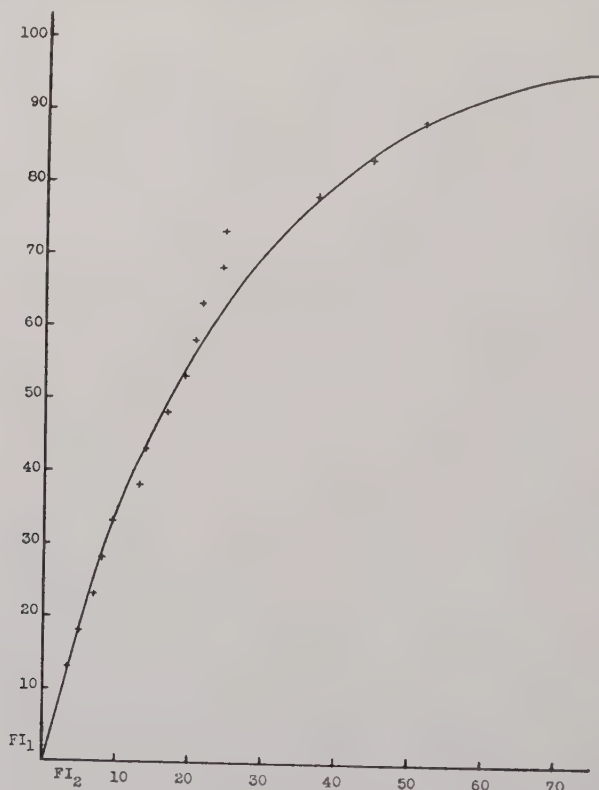


FIG. 4. Relation of frequency index for the 1 sq. m. quadrats to that for the 0.1 sq. m. quadrats.

of the frequency index of the smaller square to the abundance of the larger, where FI_1 and n_1 represent the frequency index and abundance respectively for the larger, FI_2 and n_2 the same quantities for the smaller, and a_1 and a_2 the area of the respective quadrats, may be expressed as:

$$FI_1 : n_1 = FI_2 : FI_2(a_1/a_2) \text{ or,} \\ n_1 = FI_2(a_1/a_2).$$

This relationship is shown in table V, where the first two columns represent the paired frequency indices from figure 4. The third column contains the

TABLE V. *The relation between the frequency index of 0.1 sq. m. quadrats and abundance for the 1 sq. m. quadrats*

Paired frequency indices from figure 4		Abundance	
FI ₁	FI ₂	n ₁ from fig. 2	FI ₂ × 10
5	1	13	10
15	4	40	40
25	7	72	70
35	11	107	110
45	15	148	150
55	20	197	200
65	26	260	260
75	34	337	340
85	46	465	460
95	73	735	730

respective abundances for these frequency indices as read from figure 2. In the last column, the frequency indices for the small quadrat multiplied by 10 are given. These figures show a very close agreement throughout the entire range when the averages of a great many species are considered. Individual species on a single plot show varying degrees of deviation from this general trend, but such deviations are usually consistent for both the counted and estimated abundance values.

PREDICTION OF ABUNDANCE BASED ON FREQUENCY INDICES OBTAINED FROM QUADRATS OF VARIOUS SIZES

As there is a high degree of correlation between frequency indices obtained by quadrats of various sizes, it is possible for the size to be adjusted to the character of vegetation and the purposes of the investigation. In some cases it may be that a general picture of the relative abundance of the various species is all that is desired. In other cases, as for example in range research, it is important to determine the differences in abundance of the most common species. In both of these cases quadrats should be used of such a size as to give the greatest range for the species under consideration.

To illustrate the differences in the range of frequency indices for different degrees of abundance, the paired frequency indices from figure 4 and the calculated abundance on 100 sq. m. are shown in the first three columns of table VI. The last two columns represent the difference in abundance divided by the differences in the respective frequency indices for the 1 sq. m. and 0.1 sq. m. quadrats.

In order to have a common basis for comparison, the abundance was computed on the basis of 100 1 sq. m. quadrats. As the n_1/FI_2 ratio, as shown above, is 10, the figures in the last column show a constant value approaching 10. The deviations are due to the inability to read the curves closer and also, because frequency indices were not carried into decimals.

For the smaller degrees of abundance, the ratio n/FI is much smaller for

TABLE VI. *Range in frequency indices for the 1 sq. m. and 0.1 sq. m. quadrats*

Paired frequency indices from figure 4		Abundance on 100 sq. m.	<i>n</i> /FI ratio	
1 sq. m.	0.1 sq. m.		1 sq. m.	0.1 sq. m.
5	1	13	2.7	9.0
15	4	40	3.2	10.7
25	7	72	3.5	8.8
35	11	107	4.1	10.2
45	15	148	4.9	9.8
55	20	197	6.3	10.5
65	26	260	7.7	9.6
75	34	337	12.8	10.7
85	46	465	27.0	10.0
95	73	735		

the 1 sq. m. quadrats but as the degree of abundance becomes greater, the *n*/FI ratio of the 1 sq. m. quadrats approaches that for the 0.1 sq. m., and somewhere between 75 and 85, the ratio of the latter becomes smaller than the former. As it is advantageous to have the *n*/FI ratio as low as possible, it would seem preferable to use a 1 sq. m. quadrat for all species with a frequency index on the 1 sq. m. quadrats of 80 or less. This represents an average abundance of about four individuals on each square meter. If more than an average of four plants are present on each square meter, a smaller quadrat would appear to yield more satisfactory results. Under the average conditions of the present study, 85 per cent of the species show a frequency index of 80 per cent or less.

Whether or not it would be worth while to use a smaller quadrat, would depend in part on the purpose of the investigation. In order to determine the relative numerical importance of the individual plants representing the species falling in the various classes, the number of individual plants which might be expected within each class on 100 1 sq. m. quadrats was computed on the basis of the average plant population. These figures based on the average percentages for all plots are shown in table VII.

TABLE VII. *Number of species and individual plants by frequency index classes*

Frequency index class	Number of species	Number of plants on 100 sq. m.	Per cent of total
1- 20	22.40	605	15
21- 40	4.55	400	10
41- 60	3.80	654	17
61- 80	2.80	832	21
81-100	2.45	1444	37
Total	35.00	3935	100

The number of individual plants was computed by multiplying the number of species within the class by the average abundance for the class. The greatest number of species is found in the lowest frequency class, but the average abundance of these species is low, so that only 15 per cent of the total number of individual plants are included in this class. The highest frequency class, even though it has the smallest number of species, includes more than a third of the total number of individuals. From a range research viewpoint, this highest class is very significant as it quite commonly includes the most important forage plants. Changes and variations in this class may also be of considerable ecological significance. Other things being equal, variations in abundance within this class would be measured more accurately by the 0.1 sq. m. quadrats than the 1 sq. m. quadrats. The range in frequency indices of 20 for the 1 sq. m. for the relative abundance of the various species in this class, is contrasted with a frequency index range of 60 for the same species when based on the 0.1 sq. m. quadrats.

There is a considerable advantage in the use of a double frame for the determination of frequency indices. The two sets of frequency indices serve to some extent as a check on each other: the larger quadrats give a better differentiation of the less abundant species; the smaller quadrats give a better differentiation of the more abundant species; and finally, the frequency indices of the smaller frame, when multiplied by a suitable factor, give an approximation of the abundance of the various species found on the larger quadrats.

CONCLUSIONS

1. Under ideal conditions, there is a high degree of correlation between frequency index and abundance. Under field conditions, although the relationship between frequency index and abundance is somewhat altered, there is still a high degree of correlation. Under both conditions, abundance can be calculated for a given frequency index by means of the proper curve or equation.

2. There is a high degree of correlation between the frequency indices obtained simultaneously for 1 sq. m. and 0.1 sq. m. quadrats. Furthermore, the frequency index for 0.1 sq. m. quadrats multiplied by 10 approximates the abundance on the 1 sq. m. quadrats.

3. The 1 sq. m. quadrat gives the lowest n/FI ratio for the less abundant species, and 0.1 sq. m. quadrat gives the lowest for the more abundant species. The size of the quadrat used should be determined by the character of the vegetation and the purpose of the study.

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